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# Microbial biomass, activity and soil respiration in relation to secondary succession

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With 3 figures

**Synopsis:** *Original scientific paper*

Microbial biomass ($C_{mic}$), microbial activity (SRA) and soil respiration (SR) were studied in a secondary successional row represented by an intensively cultivated field, by 2 – 10 years uncultivated fields (fallow and meadow, respectively) and by an oak forest. Regular monthly observations were made over 3 years. $C_{mic}$ and SR were lowest in the fallow and field soils and increased according to soil organic carbon content from 0.34 to 0.55 mg $C \cdot g^{-1}$ and from 0.019 to 0.034 mg $CO_2 - C \cdot g^{-1} \cdot d^{-1}$, respectively. On the contrary, SRA was lowest in the meadow soil (0.068 mg $CO_2 - C \cdot mg\ C^{-1} \cdot d^{-1}$) but reached the highest values in the field (0.113 mg $CO_2 - C \cdot mg\ C^{-1} \cdot d^{-1}$). Temporal fluctuations of $C_{mic}$ and SRA decreased in the order field – fallow – meadow and forest.

The $C_{mic}$ and SRA variations, turnover rate of $C_{mic}$, and the portion of $C_{mic}$ in the soil organic carbon are discussed.

**Key words:** Secondary succession, field, fallow, meadow, forest, microbial biomass, microbial activity, soil respiration, soil organic carbon, temporal fluctuation, turnover rate.

## 1. Introduction

Organic matter is an essential component of soil fertility and microorganisms play a vital role in its maintenance and regeneration. Organic matter, as well as quantity and activity of microorganisms, represent sensitive indicators related to processes of soil genesis (POWLSON *et al.*, 1987). At present, great attention is given to the microbial biomass, respiration and enzyme activities of intensively cultivated soils. Studies are based in most cases on comparison of agroecosystems with different agricultural practices: crop rotation, tillage system, manuring and fertilization (e.g. CARTER & KUNELIUS, 1986, SARATHCHANDRA *et al.*, 1988). However, relatively less work has been done on the evolution of the soil biotic properties in connection with secondary succession. Secondary succession is accompanied by changes in principal characteristics of plant communities (species composition, primary production and biomass, vertical structure, etc.) and by changes in soil physical and chemical properties (BUSH & AUKEN, 1986), in soil respiration (MATHES & SCHRIEFER, 1985) and nitrification (VITOUSEK *et al.*, 1989).

The aim of this study is to estimate microbial biomass, microbial activity and soil respiration in soils at four secondary successional stages.

## 2. Materials and methods

Regular monthly measurements of soil respiration (SR), microbial biomass ($C_{mic}$) and microbial activity (SRA) were made during the period of May 1986 – February 1989 at each of the following plots representing a secondary successional row. These were field [intensively cultivated field with crop

Table 1. Characteristics of soil conditions.

| plot | layer | moist.[1] | | temp.[1] | | pH[1] | $C_{org}$[1] | N[1] | P[1] | C/N[1] |
|---|---|---|---|---|---|---|---|---|---|---|
| | cm | % | V[2] | C | V[2] | | % | % | % | |
| field | 0– 5 | 18.2 | 33 | 6.4 | 95 | 5.7 | 1.5 | 0.13 | 0.088 | 11.2 |
| | 5–10 | 16.5 | 20 | | | 5.8 | 1.4 | 0.13 | 0.103 | 10.5 |
| fallow | 0– 5 | 16.7 | 29 | 6.9 | 94 | 5.9 | 1.3 | 0.10 | 0.093 | 12.5 |
| | 5–10 | 15.5 | 27 | | | 6.1 | 1.1 | 0.13 | 0.080 | 8.1 |
| meadow | 0– 5 | 26.0 | 25 | 6.9 | 86 | 5.3 | 2.9 | 0.29 | 0.086 | 9.1 |
| | 5–10 | 20.5 | 19 | | | 5.3 | 2.9 | 0.10 | 0.073 | 10.2 |
| forest | A* | 25.1 | 40 | 7.1 | 75 | 5.2 | 4.9 | 0.95 | 0.090 | 5.7 |
| | B** | 15.1 | 37 | | | 4.6 | 2.4 | 0.22 | 0.060 | 10.9 |

[1] = mean values;
[2] = coefficients of variation (%);
* = humus horizon;
** = mineral horizon.

rotation wheat (210 kg NPK $ha^{-1}$), potatoes (5000 kg farmyard manure $ha^{-1}$), barley (210 kg NPK $ha^{-1}$)]; 1–3 years old fallow (the same field where the cultivation was finished in 1985); meadow (field uncultivated 8–10 years) and forest (60–70 years old subclimax forest with the dominance of *Quercus robur* L.). The plots were situated near the village Chelčice in Southern Bohemia, in an area characterized by a mean annual precipitation of 605 mm, a mean annual temperature of 7.3. °C and by a cambisol soil type. Detailed soil characteristics of the studied plots are given in table 1.

Soil samples were taken from two different layers (0–5 and 5–10 cm) in the field, fallow and meadow, and humus and mineral layers in the forest soil, with a sampling corer (area 10 $cm^2$). Each sample was composed from five evenly distributed subsamples mixed together.

Analyses of $C_{mic}$ and SR in fresh samples were made within 24 h of sampling. $C_{mic}$ was measured with the chloroform fumigation incubation method (JENKINSON & POWLSON, 1976) modified by CHAUSSOD & NICOLARDOT (1982). Thirty grams of soil from which stones, roots and plant debris were removed were moistened to 50% WHC and exposed to alcohol free $CHCl_3$ for 20 h. The $CHCl_3$ vapours were removed by repeated evacuation using a vacuum pump. Samples were inoculated with 1 ml of soil suspension (1:10). Incubation in 300 ml bottles with a rubber stopper was for 14 days. $CO_2$ production was measured by the absorption method after 7 and 14 days. SR was measured in unfumigated soil as $CO_2$ production after 10 days incubation at 25 · °C. SRA was expressed as $CO_2$ production per unit of $C_{mic}$ and unit time – mg $CO_2$ – C mg $C^{-1}$ $d^{-1}$. All results were recalculated per gram of dry soil (drying 6 h at 105 · °C).

Soil organic carbon ($C_{org}$) was measured monthly using Tjurin's method modified by BELČIKOVA (1975).

The differences among plots were evaluated by means of the analysis of variance (two way ANOVA, $P < 0.05$) and by linear correlation between characteristics. Seasonal fluctuation of $C_{mic}$, SRA and SR as well as the fluctuation of soil moisture and temperature were characterized by means of the coefficient of variance.

## 3. Results

### 3.1. Microbial biomass ($C_{mic}$)

The average value of $C_{mic}$ was highest in the meadow soil and decreased in the sequence forest, field, fallow (table 2). On the contrary, the proportion of $C_{mic}$ in $C_{org}$ was highest in the fallow soil and decreased from the field to the meadow and forest (table 2). Differences between layers were insignificant in the field, fallow and meadow soils in contrast to the significant differences in the forest soil. Temporal fluctuation of $C_{mic}$ characterized by the coefficient of variance was lower in the forest and meadow soils than in the field and fallow

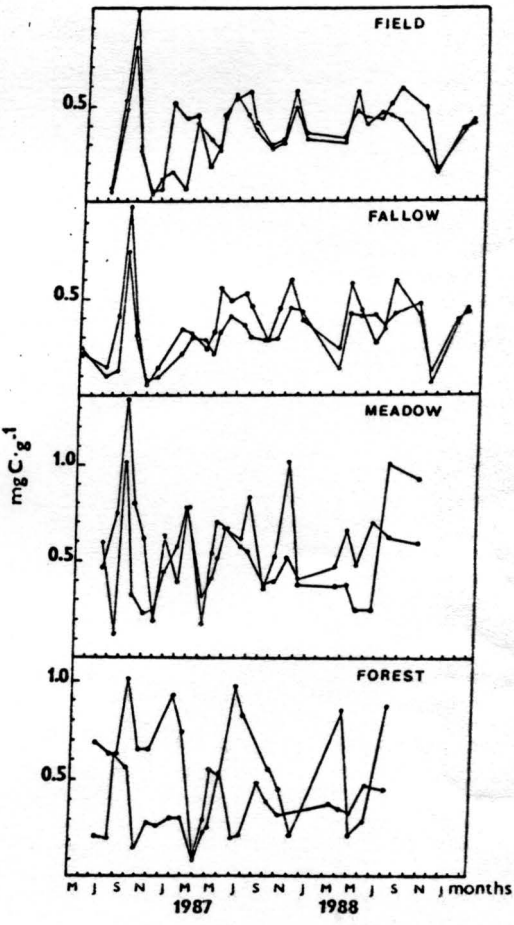


Fig. 1. Temporal fluctuation of microbial biomass in the field, fallow, meadow and forest soils in the layers 0–5 (—o—) and 5–10 cm (—●—).

soils in both investigated layers (table 2). Temporal changes of $C_{mic}$ in the field, fallow and meadow soils were the same in both investigated layers but this was not true for the $C_{mic}$ in the forest soil (fig. 1). $C_{mic}$ in the field and fallow were significantly different from the meadow, as was the meadow $C_{mic}$ from that in the forest.

A positive correlation was obtained between average values of $C_{mic}$ from individual plots and layers and $C_{org}$ ($r = 0.737$, $n = 8$) and between $C_{mic}$ and soil moisture ($r = 0.986$, $n = 8$). $C_{mic}$ to $C_{org}$ ratio was negatively correlated with $C_{org}$ ($r = 0.798$, $n = 8$).

## 3.2. Microbial activity (SRA)

On the average SRA was highest in the field soil and lowest in the meadow soil (table 2). The difference in SRA between plots was not significant as a consequence of the high

Table 2. Values of microbial biomass ($C_{mic}$ in mg $C \cdot g^{-1}$), microbial activity (SRA in mg $CO_2-C \cdot mg\ C^{-1} \cdot d^{-1}$) and soil respiration (SR in mg $CO_2-C \cdot g^{-1} \cdot d^{-1}$) in the field, fallow, meadow and forest soils in the layers 0–5 and 5–10 cm.

| plot | layer (cm) | $C_{mic}$[1] | V[2] (%) | SRA[1] | V[2] (%) | SR[1] | V[2] (%) | $C_{mic}$-to-$C_{org}$ (%) |
|---|---|---|---|---|---|---|---|---|
| field | 0– 5 | 0.39 | 51 | 0.111 | 160 | 0.022 | 27 | 2.6 |
| | 5–10 | 0.34 | 47 | 0.115 | 164 | 0.020 | 30 | 2.4 |
| | 0–10 | 0.37 | 49 | 0.113 | 161 | 0.021 | 29 | 2.5 |
| fallow | 0– 5 | 0.38 | 50 | 0.091 | 120 | 0.024 | 38 | 2.9 |
| | 5–10 | 0.31 | 48 | 0.079 | 129 | 0.015 | 60 | 2.8 |
| | 0–10 | 0.34 | 49 | 0.087 | 121 | 0.019 | 53 | 2.9 |
| meadow | 0– 5 | 0.60 | 48 | 0.090 | 78 | 0.042 | 33 | 2.1 |
| | 5–10 | 0.50 | 38 | 0.047 | 77 | 0.019 | 32 | 2.6 |
| | 0–10 | 0.55 | 46 | 0.068 | 85 | 0.031 | 52 | 2.4 |
| forest | A* | 0.60 | 43 | 0.102 | 55 | 0.054 | 39 | 1.3 |
| | B** | 0.33 | 39 | 0.060 | 73 | 0.016 | 31 | 1.4 |
| | A–B | 0.46 | 52 | 0.081 | 67 | 0.034 | 71 | 1.4 |

[1] = mean value;
[2] = coefficient of variation;
* = humus horizon;
** = mineral horizon.

temporal variability (fig. 2). Temporal fluctation of SRA was much higher than for $C_{mic}$. Coefficient of variance for SRA ranged between 73 and 164%, whereas for $C_{mic}$ only between 38 and 51% (table 2). Temporal changes of SRA were the greatest in the field soil and decreased from fallow to meadow and forest soil (table 2, fig. 2). Average values of SRA from individual layers are shown in table 2. The differences of SRA between layers increased in the sequence field, fallow, meadow and forest but were significant only for the meadow and forest. No correlation between SRA and $C_{org}$ or between SRA and soil moisture was observed. SRA was negatively correlated with $C_{mic}$ ($r = -0.446$, $n = 210$).

### 3.3. Soil respiration (SR)

SR was highest in the forest soil and decreased from the meadow to the field and fallow (table 2). SR in the field and fallow soils was significantly different from SR in the meadow and forest soils. SR in the upper layers at all plots reached higher values than in the deeper layers (table 2, fig. 3). The differences between layers, which increased in the sequence field, fallow, meadow and forest, were significant at all investigated plots. Temporal fluctuation of SR, except in the deeper layer of fallow, was lower than the fluctuation of $C_{mic}$ and SRA (fig. 3, table 2). A positive correlation was obtained between average values of SR and $C_{org}$ from individual plots and layers ($r = 0.863$, $n = 8$) and between SR and soil moisture ($r = 0.891$, $n = 8$), but between SR and SRA there was no significant correlation. Low but significant correlation was ascertained between SR and $C_{mic}$ ($r = 0.414$, $n = 210$).

## 4. Discussion

In accordance with the results of SCHNÜRER *et al.* (1985), WEST *et al.* (1988), average values of $C_{mic}$ in our experimental soils depend on $C_{org}$ content and on soil moisture.

No seasonal trends could be detected in the investigated biological characteristics. This has two explanations.

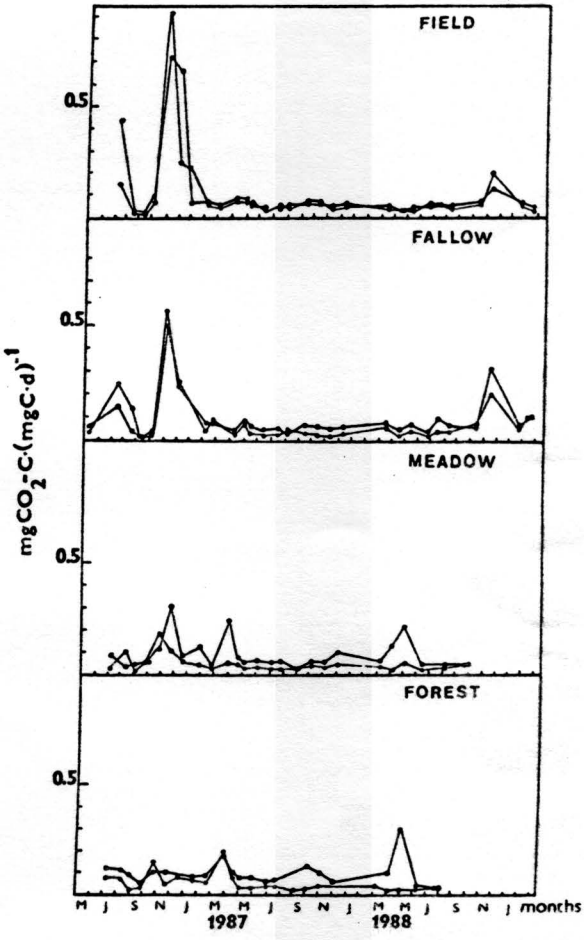


Fig. 2. Temporal fluctuation of microbial activity in the field, fallow, meadow and forest soils in the layers 0–5 (—○—) and 5–10 cm (—●—).

(1) No regular summer long-term period of drought occurred during the course of our observations. The soil moisture dropped below 10% WHC only on one sampling date. The coefficient of variance characterizing the temporal moisture fluctuation varied between 20 and 40%. Temporal fluctuation in $C_{mic}$ is not simply a consequence of variations in the organic C input but depends on the combined effects of moisture and temperature and the availability of substrates. Changes of $C_{mic}$ were most consistently related to the fluctuation of temperature and the rate of changes is dependent on the temperature and/or initial moisture content. Similar results were reported by CAMPBELL & BIEDERBECK (1976), MCGILL *et al.* (1986).

(2) The soils were not continuously frozen during the winter seasons. For example the increase of $C_{mic}$ in January and February 1986 could be explained by the increase in soil temperature and thus by the thawing of previously frozen soil.

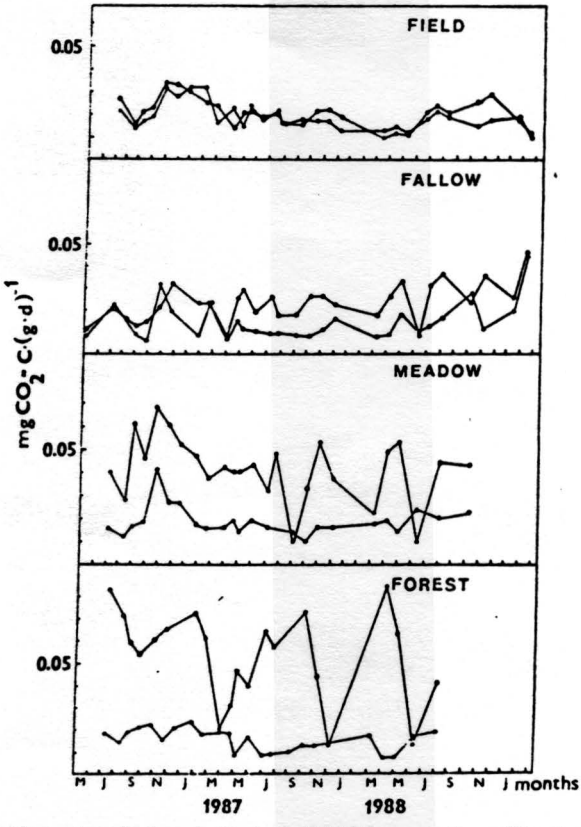


Fig. 3. Temporal fluctuation of soil respiration in the field, fallow, meadow and forest soils in the layers 0–5 (—○—) and 5–10 cm (—●—).

$C_{mic}$ during the year, and thus the turnover rate, is related to growth and death of microorganisms. A minimal estimate of turnover can be obtained by dividing the total measured losses in $C_{mic}$ by the average quantity of $C_{mic}$ present. Losses were taken as negative changes in $C_{mic}$ between sampling dates (McGILL *et al.*, 1986). The turnover rate calculated in this way was 2.1 times a year in the field soil, 1.9 in the fallow soil, 1.6 and 1.4 in the meadow and forest soils, respectively. The turnover rate is influenced by microbial activity. There is a tendency for a slightly higher turnover rate in the field and fallow than in the meadow soils. Both average microbial activity and its temporal fluctuations were also higher in these soils. The higher turnover rate and higher SRA could be due to the effect of agricultural practices, and to the higher fluctuation of environmental conditions (especially moisture and temperature) in the field and fallow soils compared with that in the meadow soil, and also to differences in the composition of the microbial community.

Our estimate of turnover rate is comparable the values of JENKINSON & LADD (1981) and McGILL *et al.* (1986) but seems to be low in relation to the doubling time for microorganisms. Doubling time of microbial population calculated from various experiments has varied from 1 to 24 days (DOMSCH *et al.*, 1983). These data are mainly a reflection of doubling time of bacterial populations in the growing stage. However, the soil microbial

community is composed not only of growing bacteria and fungi but also of microorganisms in the dormant stage. A number of studies have suggested that part of microbial biomass in soil is dormant owing to unfavourable soil conditions (ANDERSON & DOMSCH, 1985, TESAŘOVÁ, 1988). Low values of turnover rate may therefore indicate the accumulation of dormant cells.

Turnover of $C_{mic}$ requires a sufficient C input into the soil for regrowth. The average flow of C through $C_{mic}$ (determined as turnover rate × average $C_{mic}$) at investigated plots in the top 10 cm was 70–97.7 g $C \cdot m^{-2} \cdot a^{-1}$. This would require C input of 168–251 g $C \cdot m^{-2} \cdot a^{-1}$ for $C_{mic}$ maintenance and $C_{mic}$ production. Estimated C input from plants (above-ground plant matter, roots and exudates) was 202–399 g $C \cdot m^{-2} \cdot a^{-1}$ (table 3).

The C input the field and fallow soils seems to be quite low in view of the fact that the calculated total annual C input would be sufficient only for maintenance and production of $C_{mic}$ in the 10 cm top layer and cannot support the metabolic demands of the total biomass ($C_{mic}$ in the whole soil profile as well as soil fauna). Assuming that $C_{mic}$ also utilizes soil organic matter as the C source (LYNCH & PANTING, 1980) the $C_{org}$ content should decrease. In the course of the investigated period the $C_{org}$ content did not change in the field soil where the farmyard manure was added in 1987. However, the $C_{org}$ content decreased from 1.4% to 1.2% in the fallow soil during the first two years of succession (GORDIENKO, pers. comm.). These estimates are subject to the following inaccuracies:

(a) The calculations of C inputs from plant litter were only approximate.

(b) The estimated turnover rates were subject to errors and more precise estimation is possible only by using labelled C (MCGILL *et al.*, 1986).

(c) The efficiency of utilization of substrate in dependent on the composition of the microbial community, on environmental conditions and on the quality and quantity of organic substrate (JENKINSON & LADD, 1981).

(d) Maintenance energy of an active population is different from that of domant population (ANDERSON & DOMSCH, 1985). Thus all calculated values must be considered approximate.

The $C_{mic}$-to-$C_{org}$ ratio appeared to be negatively correlated with $C_{org}$. These results are in accordance with VORONEY *et al.* (1981). PARTON *et al.* (1984) assumed the $C_{org}$ was composed of fractions ranging from very active to passive. Although $C_{org}$ declines with

Table 3. The estimation of annual C input into the studied soils and the estimation of C demands for maintenance and production of microbial biomass.

| | field | fallow | meadow | forest |
|---|---|---|---|---|
| annual C input: ($g\ C \cdot m^{-2} \cdot a^{-1}$) | | | | |
| from above-ground biom.* | 161 | 110 | 199 | 239 |
| from roots and exudates** | 40 | 99 | 300 | 135 |
| | ∑ 201 | 209 | 499 | 374 |
| $C_{mic}$ demands: ($g\ C \cdot m^{-2} \cdot a^{-1}$) | | | | |
| for maintenance+ | 195 | 170 | 177 | 120 |
| for production++ | 56 | 44 | 62 | 48 |
| | ∑ 251 | 214 | 239 | 168 |

* = 0.6 · above-ground biomass at the time of maximal development of vegetation, in the forest only herb layer was considered;

** = calculation in accordance to DAHLMAN & KUCERA (1965) and COLEMAN (1973);

\+ = efficiency of utilization 50%;

++ = average value $C_{mic}$ · maintenance coefficient 0.00013.

cultivation, the most active fractions (microorganisms and their metabolites) are replenished from new residues and so may increase proportionally at the expense of less active fractions. INSAM *et al.* (1989) proposed that the equilibrium function allows the prediction of $C_{mic}$-to-$C_{org}$ ratio in a wide range of climates and soils ($y = 18.18 + 108.3^{-6.728x}$, where x = precipitation/evaporation). Deviation of the $C_{mic}$-to-$C_{org}$ ratio from this equilibrium for any given soil in corresponding conditions would reflect the stage of soil development. The $C_{mic}$-to-$C_{org}$ ratio for our climatic conditions was 1.82. Higher values of this ratio in the field, fallow and meadow soils would indicate a "young" site in the early stage of carbon accumulation. The field and fallow soils can be considered a "young" site also from the point of view of SRA. INSAM & HASELWANDTER (1989) proposed that energetic optimalization during ecological succession may occur at the soil microbial community level. The release of $CO_2$ per unit biomass and time (SRA) was higher for $C_{mic}$ from "young" sites as compared to "mature" ones. A similar tendency was observed in the present study. The average value SRA in the field and fallow soils was higher than that in the meadow and forest soils (table 2).

The positive correlation between SR and $C_{mic}$ obtained in the present study was observed by ROSS *et al.* (1980) and VEKEMANS *et al.* (1988). ROSS *et al.* (1984) observed negative correlation between SR and $C_{mic}$, while SARATHCHANDRA *et al.* (1988) showed no statistically significant relationship. This apparent discrepancy may be explained by the complex character of SR. Soil respiration (SR) calculated per unit weight of soil is a multiple of $C_{mic}$ and SRA. Thus a high SR can be caused by high $C_{mic}$ with low SRA as well as by low $C_{mic}$ with high SRA or high $C_{mic}$ and SRA. In this study SRA is expressed as respiration per unit $C_{mic}$ and time. SRA calculated in this way was negatively correlated with $C_{mic}$. The relationship between SRA and $C_{mic}$ has been discussed by ŠANTRŮČKOVÁ & STRAŠKRABA (1991).

## 5. Conclusions

(1) $C_{mic}$ and SR were lowest in the fallow and field soils and increased according to $C_{org}$ content. This is in agreement with the reduction of C input and with the increase of the mineralization rate in arable soils compared with natural soils.

(2) The decrease of the average value of SRA and the $C_{mic}$-to-$C_{org}$ ratio relate to the energetic optimalization of the soil microbial community level during secondary succession.

(3) Temporal fluctuation of $C_{mic}$ and SRA decreased in the order of field – fallow – meadow and forest. This may be explained by the decrease of temporal fluctuation of soil abiotic and biotic conditions and increases in the diversity of the microbial community.

(4) Differences in $C_{mic}$, SRA and SR between investigated soil layers (0–5 and 5–10 cm) increased from the field to meadow and forest.

(5) The C input for the maintenance and production of $C_{mic}$ that decreased from 251 (field) to 214 g $C \cdot m^{-2} \cdot a^{-1}$ (fallow) and was low in the first years of succession. Both $C_{mic}$ and $C_{org}$ also decreased. However, the $C_{org}$ content as well as $C_{mic}$ increased in the meadow soil in accordance with higher plant production.

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